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THE GENERA OF AMARANTHACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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AMARANTHACEAE A. L. Jussieu, Gen. Pl. 87. 1789,
"Amaranthi," nom. cons.

(AMARANTH FAMILY)

Annual or perennial herbs, often woody at the base, infrequently lianas [or shrubs or trees]; stems erect to decumbent, trailing, or climbing, simple or much branched, unarmed or rarely spinescent, glabrous to densely pubescent, [very rarely fleshy and/or articulated], usually from a stout taproot. Leaves alternate or opposite, simple and usually entire, sometimes undulate, infrequently serrulate or shallowly lobed, [very rarely reduced to scales or absent], long-petiolate to sessile; stipules absent. Inflorescences of compact cymes or clusters arranged in axillary or terminal, simple or compound spikes, panicles, heads, or rarely racemes, or the flowers solitary; foliage leaves often reduced and bractlike in the inflorescence; each flower subtended by 1 bract and usually 2 bracteoles, all usually scarious, often spinescent, the

¹Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum of Harvard University. This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39**: 296-346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information from extraterritorial taxa in brackets. References that I have not seen are marked by an asterisk.

This paper was initiated while I was at the Arnold Arboretum, but it has been written largely with the generous support of the Illinois Natural History Survey. In addition to the libraries of the Arnold Arboretum and the Gray Herbarium, the library of the University of Illinois has been invaluable for checking the voluminous references. The libraries and herbaria of the Field Museum of Natural History and of the Missouri Botanical Garden were also utilized in this study, and specimens of *Amaranthus* were

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bract persistent and the bracteoles either falling with the fruit or persistent. Flowers quite small, regular, perfect or imperfect (the plants then monoecious, dioecious, or polygamous), sometimes aborted [or reduced to hooked spines]. Tepals usually 4 or 5, rarely absent, free or partly connate at the base, equal to somewhat unequal, imbricate in aestivation, usually dry and scarious or chartaceous, sometimes indurated, glabrous to densely pubescent, usually persistent around the fruit and falling either with or without it. Androecium of (1-)4 or 5 antetepalous, included (or rarely exerted) stamens; filaments free or (more commonly) basally connate into a cup or tube, the free portions linear to variously dilated, a nectariferous disc sometimes present at base of cup or tube; anthers dorsifixed, introrse, opening by longitudinal slits, either 4-locular with 2 lines of dehiscence or 2-locular with a single line of dehiscence; staminodia sometimes present in functionally carpellate flowers; pseudostaminodia present or absent, when present, of variously shaped, entire to laciniate lobes alternating with the filaments on the staminal tube; pollen grains pantoporate, trinucleate. Gynoecium of 2 or 3 united carpels; ovary superior, 1-locular, often somewhat compressed [rarely lobed]; style usually 1, terminal, elongate to very short or absent, infrequently indurate; stigmas entire and capitate or 2- or 3-lobed with the segments capitate to subulate and erect to divergent, persistent; ovules 1 or several, campylotropous or amphitropous, bitegmic, crassinucellate, inserted on short to elongate funiculi from a basal placenta and either suspended with the micropyle upward or erect with the micropyle downward. Fruit a dry, 1- to several-seeded, indehiscent, circumscissile, or irregularly dehiscent utricle or pyxis [rarely a berry or drupe]. Seeds small, mostly lenticular, subglobose, or subreniform, brown to black, erect or inverted, [sometimes enclosed by a small to large and bivalved aril], the testa usually shining, crustaceous; embryo peripheral, surrounding the mealy (farinaceous) perisperm; cotyledons incumbent; radicle superior or inferior. Embryo sac development of the *Polygonum* type. TYPE GENUS: *Amaranthus* L.

About 65 genera and 900 species, nearly cosmopolitan in distribution, but evidently absent from arctic and alpine habitats, most abundant in the tropics, subtropics, and warm-temperate regions. The number of genera is usually

kindly lent by the University of Florida. Special thanks go to Dr. Carroll E. Wood, Jr., who reviews each paper in the Generic Flora series as thoroughly as though it were his own. The editorial expertise of Dr. Stephen A. Spongberg and of Ms. Elizabeth B. Schmidt is also appreciated. Ms. Laurie B. Feine has kindly read the treatments of *Amaranthus*, *Celosia*, and *Gomphrena* and has offered several suggestions and references. The plates of *Achyranthes* and *Iresine* were drawn by Karen Stoutsenberger, that of *Amaranthus* by LaVerne Trautz, and that of *Alternanthera* by Rachel A. Wheeler. All were made under the supervision of Dr. Wood, who also planned and prepared the dissections; all were prepared with the support of grants from the National Science Foundation. Living and alcohol-preserved material for the illustrations was supplied by George Avery, R. B. Channell, T. S. Elias, the late H. F. L. Rock, Allan Strahler, and C. E. Wood, Jr. The manuscript was typed by Betty Nelson, and Robbin C. Moran rechecked many of the references.

estimated to be about 65, but generic limits are not easily defined in some groups, and fewer than 60 or more than 70 genera could be recognized. At present, there seems to be a trend toward consolidation, and further study of some poorly known genera from Africa and South America may lead to more mergers. Numerous species occur in arid habitats; many are weeds; a number are found in harsh situations such as sandy, calcareous, saline, gypseous, or serpentine soils; some are found in undisturbed tropical forests; and a few are maritime, aquatic, or semiaquatic. The family is most diverse in Africa south of the Sahara Desert, southwestern North America, and Central and South America. Approximately 25 genera (about 100 species) are restricted to Africa; 16 of these have but one or two species, while the largest (*Hermbstaedia* Reichenb. and *Pandiaka* (Moq.) Hooker f.) contain about 20 species each. The great majority of genera endemic to Africa belong to subtribe Achyranthinae (see below). About 13 genera (depending on the limits adopted) are essentially endemic to the Americas and the Galapagos Islands. Three of these (*Pleuropetalum* Hooker f., *Chamissoa* HBK., and *Pseudoplantago* Suesseng.) belong to the Amaranthoideae, the remaining ten to Gomphrenoideae-Gomphreneae. Seven of the American genera are monotypic or have only two species, but *Alternanthera* Forsskål, with an estimated 170 species, is the largest in the family. Two genera are largely endemic to Madagascar, two to the Hawaiian Islands, and three (including *Pitilotus* R. Br., which is perhaps the second largest in the family, with an estimated 100 species) to Australia. Only *Cyathula* Blume, *Iresine* P. Br., *Gomphrena* L., *Amaranthus* L., *Alternanthera*, and *Philoxerus* R. Br. were originally indigenous in both Eastern and Western hemispheres. Eleven genera (in the inclusive sense) and about 76 species of Amaranthaceae occur in the continental United States, and all of these genera except *Dicraurus* Hooker f. occur in the Southeast.

The Amaranthaceae were studied extensively by Moquin-Tandon (1849) for De Candolle's *Prodromus* and by Schinz (1893, 1934) for both editions of Engler & Prantl's *Die Natürlichen Pflanzenfamilien*. A number of new species and genera were described in numerous papers by Suessenguth, and the African and Madagascan genera were recently reviewed by Cavaco (1962, 1974). Revisionary papers have been published recently by Mears, Pedersen, Sohmer, and Townsend.

The Amaranthaceae are usually divided into subfamilies Amaranthoideae (anthers 4-locular at maturity with two lines of dehiscence) and Gomphrenoideae Schinz (anthers 2-locular at maturity with a single line of dehiscence). Schinz (1934) further divided the subfamilies into the following tribes and subtribes:

- Amaranthoideae:** CELOSIEAE
 AMARANTHEAE: Amaranthinae and Achyranthinae
Gomphrenoideae: BRAYULINEAE: Brayulineinae and Tidestromiinae
 GOMPHRENEAE: Froelichiinae and Gomphreninae

Cavaco (1962) proposed a somewhat different scheme, recognizing four

subfamilies and five tribes, but no subtribes; unfortunately, the new categories he proposed are invalidly published since no Latin descriptions or diagnoses are either referred to or given. Cavaco's scheme, however, should be examined carefully by future monographers, since genera referred by Schinz to subtribes *Amaranthinae* and *Achyranthinae* were substantially rearranged. In the present paper the classification of Schinz is used, with the exception that, following Mears, tribe *Brayulineae* is included within the *Gomphreneae*.

The *Amaranthaceae* belong to the order *Centrospermae* (*Caryophyllales*, *Chenopodiales*), one of the most natural and clearly defined orders of flowering plants. There has been spirited debate, however, over the importance that should be given to the betalain or anthocyanin pigments. Mabry places all the families with betalain pigments in suborder *Chenopodiineae*, and the *Caryophyllaceae* and *Molluginaceae*, both of which have anthocyanin pigments, in suborder *Caryophyllineae*. Cronquist does not subdivide the order, while Thorne recognizes three suborders: *Chenopodiineae* (betalains plus anomalous secondary thickening from successive cambia), *Portulacineae* (betalains, no anomalous secondary thickening), and *Caryophyllineae* (anthocyanins and anomalous secondary thickening). In Takhtajan's most recent classification scheme, order *Caryophyllales* is divided into three suborders: *Phytolaccineae* (all but two betalain families), *Caryophyllineae* (anthocyanin families), and *Chenopodiineae* (*Chenopodiaceae* and *Amaranthaceae*—both betalain families).

The *Amaranthaceae* are very closely allied to the *Chenopodiaceae* (the two were united by Baillon), and they share a number of characteristics: anomalous secondary thickening, generally small flowers, a perianth of tepals in one whorl, pollen characters (see Nowicke, and Skvarla & Nowicke), a syncarpous and superior gynoecium usually with one ovule, distinctive centrospermous embryology, basal or free-central placentation, betalain pigments (see Mabry), and P-type form (c) sieve-element plastids (see Behnke). The *Amaranthaceae* are distinguished from the *Chenopodiaceae* by the dry, scarious bracts, bractlets, and tepals, and by the androecium usually with connate filaments and frequently with pseudostaminodia.

A new character that has been of significance in the delimitation of the *Centrospermae* is the type of plastid found in sieve elements. In most plants, these plastids accumulate starch; however, in all the families assigned to the *Centrospermae* by Mabry (1977), and only in these families, the sieve elements accumulate protein in ring-shaped bundles of filaments. The plastids of the *Amaranthaceae* and *Chenopodiaceae* lack the central crystalloid structures that are found in the other centrospermous families.

The pollen of all *Amaranthaceae* studied thus far (Handro, Livingstone *et al.*, Martin & Drew, Nair & Rastogi, Nowicke, Rădulescu, Riollot & Bonnefille, Skvarla & Nowicke, Tsukada, Vishnu-Mittre, and Zandonella & Lecocq) is pantoporate and mostly spherical. The pores are covered with various amounts of ektexine, which is developed into protruding stellate structures in *Papulia*. There are two basic subtypes of pollen, corresponding to the two subfamilies. The pollen of subfamily *Amaranthoideae* has a spinulose

and tubuliferous/punctate ectexine. (According to Nowicke, similar pollen is found in the Caryophyllaceae, Chenopodiaceae, Dysphaniaceae, and Phytolaccaceae.) In subfamily Gomphrenoideae, the pores are deeply recessed, giving the pollen a reticulate or polyhedral appearance. There is considerable variation in pollen morphology within both subfamilies, and it is likely that this variation will prove to have some taxonomic significance.

Chromosome numbers have been reported for only about 20 of the ca. 65 genera of Amaranthaceae, and the vast majority of counts are of species of *Amaranthus*. Based on this small sample, the family has a wide variety of base chromosome numbers: 6, 7, 8, 9, 10, and 13—plus some multiples and combinations of these. This is in contrast to the Chenopodiaceae, which have a uniform base number of 9. Numerous ploidy levels from diploid to duodecaploid are also known in the Amaranthaceae. Several different base numbers are frequently reported within the same genus (see discussion under *Amaranthus*), some species have cytological races, and in *Digera arvensis* Förskal there are different chromosome numbers in different nuclei of pollen mother cells (Desai, 1971), which may account for the different chromosome numbers reported for the species. It seems that much remains to be learned about the cytology of the Amaranthaceae and that detailed studies at the generic or family level would be worthwhile.

Despite the weedy character of many members of the family, the Amaranthaceae are of considerable use to man. The seeds of *Amaranthus* species have been used as pseudo-cereal grains in many parts of the world, and a number of domesticated races have been developed in Central and South America. Species of *Amaranthus* and *Celosia* are also widely used as potherbs. Some species of *Amaranthus*, *Alternanthera*, and *Iresine* have colorful foliage and are cultivated as ornamentals, and species of *Gomphrena* and *Celosia* are grown for their showy inflorescences.

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KEY TO THE GENERA OF AMARANTHACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *annual or perennial herbs; leaves alternate or opposite, simple, mostly entire, exstipulate; inflorescences of cymes grouped in terminal and/or axillary spikes, panicles, heads, clusters, or racemes, bracteate and usually bibracteolate; flowers small, regular, perfect, or imperfect and the plants monoecious or dioecious; tepals usually 4 or 5, free or basally connate, equal to unequal, imbricate, scarious, chartaceous, or indurate; stamens usually 4 or 5(3), opposite the tepals; filaments free or more commonly basally connate into a cup or tube with the free portions often alternating with variously shaped pseudostaminodia; anthers dorsifixed, introrse, with 2 or 4 locules; ovary superior, 1-loculate and 2- or 3-carpellate; ovules 1 (or numerous), predominantly campylotropous, the placentation basal; fruit generally a dry, dehiscent or indehiscent utricle; seeds small, shiny, lenticular to subglobose or subreniform, the embryo peripheral around the mealy perisperm.*

- A. Leaves alternate.
 - B. Flowers perfect; ovaries with several ovules, the fruits with several seeds. 1. *Celosia*.
 - B. Flowers imperfect; ovaries with one ovule, the fruits with one seed. 2. *Amaranthus*.
- A. Leaves opposite.
 - C. Flowers imperfect; inflorescences terminal, diffuse, open panicles. 9. *Iresine*.
 - C. Flowers perfect; inflorescences terminal and/or axillary spikes, heads, or glomerules.
 - D. Inflorescences terminal, simple or compound, elongate spikes.
 - E. Inflorescences mostly interrupted, compound spikes; tepals united into a lanate perianth tube bearing lateral crests or spines. 6. *Froelichia*.
 - E. Inflorescences mostly simple spikes with the flowers progressively farther apart toward the base; tepals free or basally connate, \pm glabrous, without lateral crests or spines. 3. *Achyranthes*.
 - D. Inflorescences axillary and/or terminal heads, glomerules, or short, condensed spikes.
 - F. Inflorescences axillary glomerules or short spikes.
 - G. Indumentum of stellate trichomes. 5. *Tidestromia*.
 - G. Indumentum, when present, of simple trichomes.
 - H. Inflorescences few-flowered axillary glomerules; pseudostaminodia absent. 4. *Guilleminea*.
 - H. Inflorescences short, axillary spikes; pseudostaminodia present. 7. *Alternanthera*.
 - F. Inflorescences terminal heads or headlike spikes.
 - I. Inflorescences immediately subtended by one or more leaves.
 - J. Leaves fleshy, linear to narrowly obovate, sessile, glabrous except in the axils. 10. *Philoxerus*.
 - J. Leaves not fleshy, ovate, shortly petiolate, long-pilose at least below and on the margins. 8. *Gomphrena*.
 - I. Inflorescences not subtended by leaves. 7. *Alternanthera*.

Subfamily AMARANTHOIDEAE

Tribe CELOSIEAE Endl.

1. *Celosia* Linnaeus, Sp. Pl. 1: 205. 1753; Gen. Pl. ed. 5. 96. 1754.

Annual or perennial herbs, often woody below [or shrubs or small trees]; stems slender to stout, usually much branched, often over 1 m. tall or long, glabrous [or pubescent], erect or scandent. Leaves alternate, petiolate, often decurrent, entire [or lobed], the blades lanceolate, ovate, deltoid, or linear, symmetrical or asymmetrical; 2 small, falcate leaves (often mistaken for stipules) sometimes in the axils of normal leaves. Inflorescences terminal and also often axillary, sessile or pedunculate, solitary or clustered, continuous or interrupted spikes or fascicles [rarely cymes], usually fasciated in cultivated forms. Flowers perfect, subtended by 1 bract and 2 bractlets, brownish to (especially in cultivated forms) various shades of red, pink, yellow, purple, white, or silver. Tepals 5, distinct, \pm equal, glabrous, scarious, striate nerved, persistent and erect in fruit, imbricate in aestivation. Stamens 5; filaments united below into a membranaceous cup, the free portions subulate or filiform; pseudostaminodia usually absent but sometimes present and dentate, alternating with the free portions of the filaments; anthers dorsifixed, introrse, with 4 locules and 2 lines of dehiscence. Style 1, short, elongate [or nearly absent], sometimes indurated, terminated by 2 or 3 capitate or subulate stigmatic lobes; ovary ovoid, subglobose, or cylindrical, sessile, unilocular; ovules usually 2 to many, campylotropous, inserted at the tip of elongate funiculi attached to a basal placenta. Fruit a subglobose or ovoid, membranaceous, usually centrally circumscissile utricle. Seeds 2 to many, erect, lenticular, shiny, smooth; embryo annular around the mealy perisperm, the cotyledons linear, the radicle inferior. LECTOTYPE SPECIES: *C. argentea* L.; see P. C. Standley, N. Am. Fl. 21: 96. 1917, and also A. S. Hitchcock & M. L. Green, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 135. 1929. (Name from Greek *keleos*, burning, alluding to the color and/or appearance of the inflorescence; an ancient name adopted by Linnaeus for this genus.) — COCKSCOMB.

Perhaps 65 species, mostly of the tropics and subtropics of the Americas and Africa. Only two species are indigenous to the continental United States, while one or two other species, depending on taxonomic concepts, have been introduced and have escaped from cultivation. *Celosia nitida* Vahl, a perennial herb with a woody taproot and slender, erect, often scandent stems, occurs in coastal sand dunes and hammocks near the seashore in southern peninsular Florida and the Florida Keys, as well as in Texas, the West Indies, Mexico, and Central and South America. *Celosia Palmeri* S. Watson, a much-branched, low shrub, reaches southern and western Texas; it also occurs in northeastern Mexico.

One taxonomic complex includes *Celosia argentea* L., a wild species, and the cultivated "cockscumb," which is variously treated as a distinct species

(*C. cristata* L.), a variety (*C. argentea* var. *cristata* (L.) O. Kuntze), or a form (*C. argentea* f. *cristata* (L.) Schinz). Both taxa have escaped sporadically in our area, but neither seems to have become strongly established.

Celosia argentea was perhaps originally native to India, although it is very widespread today, either as a weed or as an escape from cultivation, from the tropics to warm-temperate regions of both hemispheres. Throughout most of its present range the species is an octoploid with $2n = 72$, although a tetraploid race (races?) has been found in eastern, western, and central India (Khoshoo & Pal, Behera & Patnaik, Desai, the last two under family references). Cultivated cockscomb thus far appears to be uniformly tetraploid with $2n = 36$. The unusual occurrence of a tetraploid cultivated species and a closely related, predominantly octoploid species has caused some interesting speculation. Grant, unaware of the tetraploid race of *C. argentea*, postulated—on the basis of cytological and morphological observations on *C. argentea* and cockscomb, F_1 and F_2 hybrids between them, and an autoallopolyploid—that *C. argentea* is an allopolyploid that arose between cockscomb and some unknown species. This hypothesis was questioned by van Steenis (see Backer, family references); and Khoshoo & Pal, after cytological and breeding studies on cockscomb and tetraploid plants of *C. argentea*, argued that cockscomb had its origin in selections made long ago from tetraploid forms of *C. argentea*. Grant presents good arguments for maintaining *C. argentea* and *C. cristata* as distinct species (a course followed in *Hortus Third*, p. 241, 1976), while Khoshoo & Pal think that the close genetic relationship within the complex, as revealed in their crossing experiments, is best reflected in a taxonomic scheme that recognizes only one species, *C. argentea*, with several varieties.

Cockscomb, which has the longest history of cultivation of any fasciated plant, is widely grown as an ornamental throughout much of the world for its colorful, fasciated inflorescences that come in many shades of yellow and red to white, orange, or deep purplish red. There are two basic inflorescence types (plumose and widely convoluted combs); within each type, the forms breed true. *Celosia argentea* is also a popular vegetable in Africa.

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Tribe AMARANTHEAE

2. *Amaranthus* Linnaeus, Sp. Pl. **2**: 989. 1753; Gen. Pl. ed. 5. 427. 1754.²

Annual [very rarely perennial], often weedy, robust herbs, sometimes woody below; stems erect, ascending, or infrequently decumbent, simple or much branched from the base, unarmed or rarely with a pair of spines at the bases of the leaves, sometimes striate and/or fleshy, green to reddish or whitish, coming from a stout taproot. Leaves alternate, entire or undulate, rhombic, lanceolate, ovate, oblanceolate, obovate, or rarely spathulate and emarginate, sometimes \pm fleshy, green to reddish or yellowish, the midrib often excurrent and sometimes spinescent; petioles usually elongate; stipules absent. Inflorescences dense terminal and/or axillary compound dichasia arranged in spikes, thyrses, panicles, or glomerules, the axis sometimes greatly thickened, the inflorescence units often subtended by reduced leaves; each dichasium subtended by a persistent, usually spine-tipped bract. Flowers small, greenish or reddish, imperfect and the plants either monoecious or dioecious. Tepals usually 3–5, or absent or rudimentary in carpellate flowers, distinct,

²See Sprague regarding the spelling *Amaranthus* vs. *Amarantus*.

membranaceous, \pm equal or the outer exceeding the inner, glabrous, the midrib faint to broad, usually excurrent and often spinescent. Stamens 3–5, absent in carpellate flowers; filaments free to the base; pseudostaminodia absent; anthers dorsifixed, introrse, with 4 locules and 2 lines of dehiscence. Style short or absent; stigmas 2 or 3, subulate, persistent; ovary ovoid, absent in staminate flowers; ovule 1, erect, the micropyle inferior, the funiculus short. Utricle 1-seeded, 2- or 3-beaked, membranaceous and circumscissile, irregularly dehiscent, or indehiscent. Seed lenticular to subglobose, smooth, shining; embryo coiled into a ring around the perisperm, the radicle inferior. (Including *Acnida* L.) LECTOTYPE SPECIES: *A. caudatus* L.; see N. L. Britton & A. Brown, *Illus. Fl. No. U. S. Canada*, ed. 2, 2: 1. 1913; also A. S. Hitchcock & M. L. Green, *Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot.* 188. 1929. (Name from Greek *amarantos*, unfading, evidently referring to the persistent, unwithering tepals; this name was applied by Ovidius and Plinius to *Celosia* and by Dioscorides and Galenus to *Helichrysum* (Compositae). — AMARANTH.

Perhaps 60 species now nearly cosmopolitan in distribution, particularly abundant as weeds in cultivated fields and other disturbed sites; the great majority of species originating in the New World. Since many species are weedy and the seeds are often carried about by man, both intentionally and inadvertently, it is difficult to say exactly how many species are indigenous or naturalized in any given area. About 26 species are native to America north of Mexico, 10 of them to the eastern United States. Approximately 13 species are introduced into the eastern United States from the western United States, Mexico, Central America, and South America. Some of these introductions are local and possibly only ephemeral, while others are now very common and widespread.

The species of *Amaranthus* are sometimes difficult to distinguish, especially for one not familiar with the group. The flowers are small, but floral characters are essential; young plants may not have mature fruits, which are sometimes needed; there are few distinguishing features for staminate plants of species of subg. *ACNIDA*; and a number of characters are qualitative. Also, some taxonomists consider amarantids mere weeds and do not take the time to examine them carefully. In any case, herbarium specimens of the genus are frequently misidentified. Collectors also tend to ignore the genus, presuming that the species are everywhere and have surely been collected from a given area before. As a result, it is likely that the geographic distributions for species of *Amaranthus* given in various floras and manuals are incomplete and/or inaccurate.

The genus can be subdivided into two subgenera: *AMARANTHUS* (plants monoecious) and *ACNIDA* (L.) Aellen ex K. R. Robertson³ (plants dioecious).

³ *Amaranthus* subgenus *Acnida* (L.) Aellen ex Robertson, comb. nov. Basionym: *Acnida* Linnaeus, *Sp. Pl.* 2: 1027. 1753; *Gen. Pl.* ed. 5. 427. 1754. TYPE SPECIES: *Acnida cannabina* L. = *Amaranthus cannabinus* (L.) Sauer. Aellen (1959, pp. 467, 474) did not give a full and complete reference for the basionym, as required after 1 January 1953 by Article 33 of the International Code of Botanical Nomenclature.

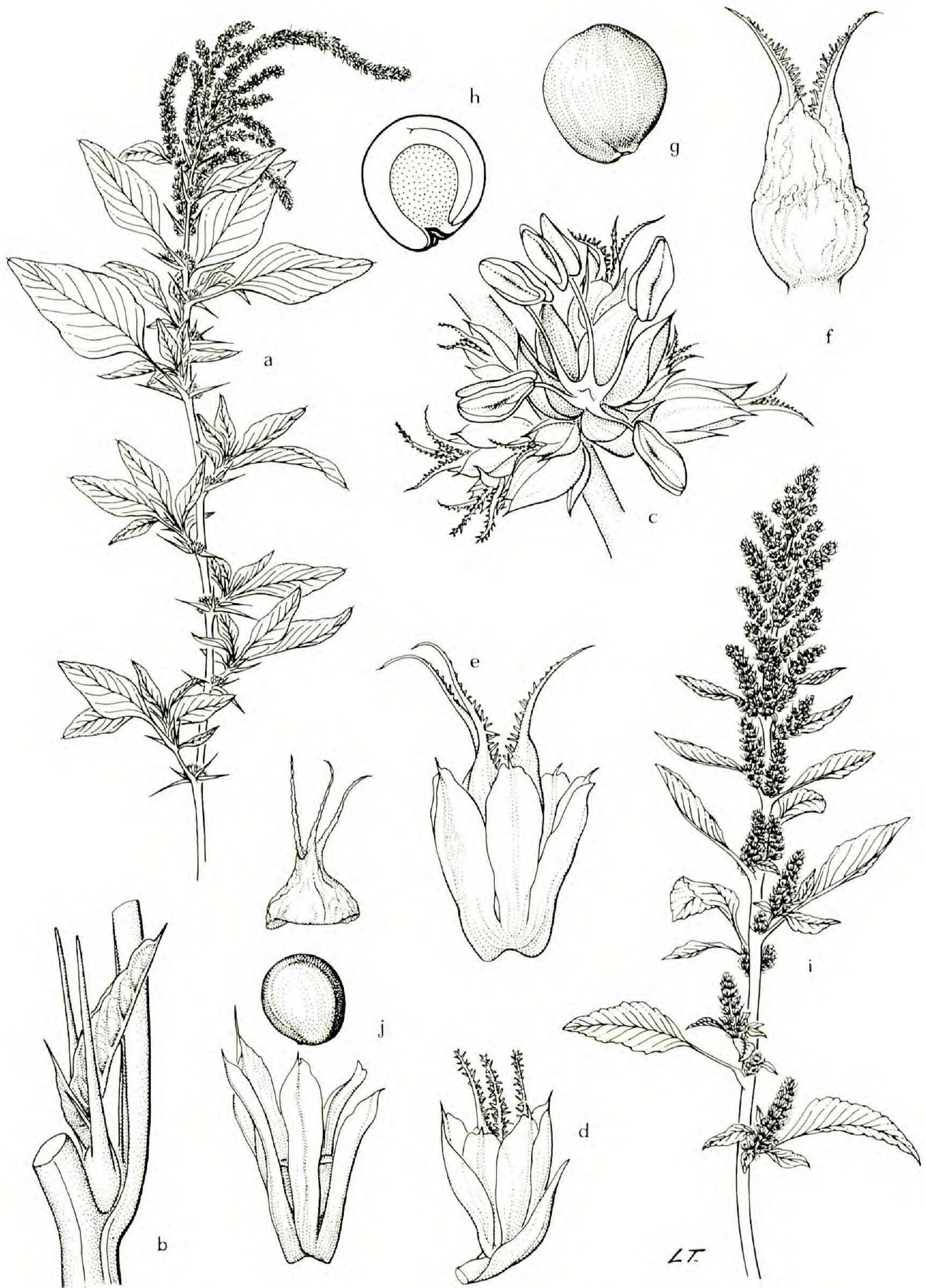


FIGURE 1. *Amaranthus*. a-h, *A. spinosus*: a, flowering stem, $\times \frac{1}{2}$; b, node with pair of axillary spines, base of petiole to extreme right, $\times 4$; c, cymule of flowers with central staminate flower at anthesis, carpellate flowers with exserted styles, $\times 8$; d, three-carpellate flower, inflorescence bract to lower right, $\times 15$; e, mature fruit with persistent and enlarged tepals, $\times 15$; f, mature, two-carpellate, indehiscent utricule, $\times 15$; g, seed, $\times 20$; h, seed

Subgenus AMARANTHUS is composed of two sections: AMARANTHUS (sect. *Amaranthotypus* Dumort.; "*Paniculati*" of Small), with large terminal inflorescences and circumscissilely dehiscent fruits; and BLITOPSIS Dumort. (group "*Crassipes*" of Small), with axillary flower clusters and mostly indehiscent fruits. Kowal (1955) proposed a third section for *A. gracilis* Desf. (= *A. viridis*) and *A. acutilobus* Uline & Bray, but no Latin diagnosis accompanied the name, which is thus invalid.

Perhaps only two species of sect. AMARANTHUS are native to the southeastern United States: *A. hybridus* L. and *A. retroflexus* L. According to Sauer (1967), both of these were riverbank pioneers in eastern North America (and westward and southwestward). They are now extremely abundant weeds in agricultural fields and waste places and, like most of our common weeds, are often taken for exotic species. *Amaranthus spinosus* L., originally of the New World tropical lowlands (Sauer, 1967), is now a pantropical weed and is common in our area, especially in barnyards and other areas where livestock is raised. A number of other species of sect. AMARANTHUS have been introduced into our area but have not yet become widely established. These include *A. hypochondriacus* L. (a pseudo-grain crop of southwestern North America derived mainly from *A. Powellii*), *A. cruentus* L. (also a pseudo-grain crop from Mexico or Guatemala, probably derived from *A. hybridus*), *A. caudatus* L. (an Andean pseudo-grain crop perhaps derived from *A. quitensis* HBK.), *A. Powellii* S. Watson (native to cordilleran North and South America), and *A. viridis* L. (a pantropical weed; incl. *A. gracilis* Desf.). Because of the weedy nature of the species of sect. AMARANTHUS, geographic ranges are not given here, since they are difficult to give precisely, being subject to frequent extensions and/or local eradications.

One, or possibly two, species of sect. BLITOPSIS are indigenous to our area, and others are introduced. *Amaranthus pumilus* Raf. is local on beach dunes from Nantucket and Martha's Vineyard, Massachusetts, southward along the coast to South Carolina. *Amaranthus polygonoides* L., a rather weedy plant of sandy soil and waste ground, occurs sporadically from Florida to Texas, and in Mexico, northern South America, the Bahamas, and the West Indies; it is not clear whether this species is indigenous in the Southeast. *Amaranthus crassipes* Schlecht., supposedly introduced from tropical America, is found along the Gulf coast from Florida to Texas; it also occurs in the Bahamas, the West Indies, and northern South America and has been introduced at seaports and along railroad tracks in the eastern United States, including Aiken Co., South Carolina. Two other species of this section are introduced weeds in our area: *A. albus* L. (*A. graecizans* of American authors, not L.), tumbleweed, originally native to the prairies and plains of central North America, but now widespread throughout the continent;

in section, perisperm stippled, $\times 20$. i, j, *A. retroflexus*: i, upper part of small plant with flowers and fruits, $\times 1/2$; j, mature, circumscissilely dehiscent utricle (pyxis) with lid at top, seed in middle, and persistent tepals and base of fruit below, $\times 12$.

and *A. blitoides* S. Watson (also *A. graecizans* of American authors, not L.),⁴ native to western and central North America but now widespread in the eastern part of the continent. *Amaranthus Blitum* L. (*A. lividus* L.) has been reported from North Carolina and Florida. (See Fillias *et al.* and Brenan for differing views on the name of this species.)

As delimited by Standley (1917, family references), Reed (1969, family references), and others, *Acnida* included those dioecious species with carpellate flowers lacking a well-developed perianth. (Dioecious species with an evident perianth were included in *Amaranthus*.) Sauer (1955) pointed out that the perianth character is inconsistent and that "the dioecious habit, which is extremely constant, is the only morphological character distinguishing this group [*Acnida*] as a whole from all the monoecious amaranths. . . . The balance of the evidence seems to show that the affinity between *Acnida* and *Amaranthus* is too great to justify maintaining them as separate genera. . . ." Sauer also included the monotypic *Acanthochiton Wrightii* Torrey of the southwestern United States and adjacent Mexico, which has broad, foliaceous bracts on the carpellate inflorescences, within *Amaranthus* as *A. Acanthochiton* (Torrey) Sauer. Although Sauer (1957) did not propose a formal taxon for the dioecious amaranths, he did consider them to be a group of related species, in the present paper placed in subgenus ACNIDA.

Subgenus ACNIDA, composed of ten species, is restricted to the New World, primarily North America, Mexico, and the Greater Antilles. Nearly all species occur in wet habitats, and four are maritime. The group has been studied extensively by Sauer (1955, 1957, 1972). Seven species occur in the southeastern United States (see distribution map in Sauer, 1957). *Amaranthus floridanus* (S. Watson) Sauer (*Acnida floridana* S. Watson), endemic to Florida, occurs mostly on coastal dunes and beaches on the eastern and western shores of peninsular Florida. *Amaranthus australis* (A. Gray) Sauer (*Acnida australis* A. Gray; including *Acnida alabamensis* Standley and *Acnida cuspidata* Bert. ex Sprengel) is found in wet areas near both fresh and salt water over much of Florida and ranges westward and southward along the coasts of the Gulf of Mexico and the Atlantic Ocean to Texas, Mexico, Venezuela, Surinam, and Brazil; it also occurs on the Greater Antilles. Individuals of *A. australis*, which is presumably annual, can become amazingly tall, and there are reports of plants up to 9 m. high (see Sauer 1955, 1972). *Amaranthus cannabinus* (L.) Sauer (*Acnida cannabina* L.), a plant of the Atlantic tidewater zone, ranges from southern Maine to northernmost Florida; it also extends inland along the Hudson and Delaware rivers. *Amaranthus tuberculatus* (Moq.) Sauer (*Acnida altissima* Riddell, *Acnida subnuda* (S. Watson) Standley) is widespread in the northeastern and midwestern United States but is absent from most of the Mid-Atlantic and Southeastern states; in our area it is found in western

⁴This species is called *A. graecizans* in many floras of the eastern United States, following Fernald (1945); but Sauer & Davidson (family references) maintain that this name is properly applied to an Old World species and that *A. blitoides* is the correct name for the plants in North America. This latter nomenclature is also used by Aellen and by Tutin (see family references).

Alabama and Tennessee and in eastern Louisiana and Arkansas. *Amaranthus rudis* Sauer (*Amaranthus tamariscinus* of authors, not Nutt.; see Sauer, 1972) occurs primarily in the midwestern United States from North Dakota eastward to Indiana and southward to eastern Tennessee, Mississippi, and Texas. *Amaranthus Palmeri* S. Watson was originally a plant of southwestern North America but is now introduced in Florida, South Carolina, Louisiana, and several Midwestern and Northeastern states; according to Sauer (1955), this probably is the weediest of the dioecious amaranths. *Amaranthus Greggii* S. Watson is known from our area only by one collection (*Thieret & Reese 10028*), from Cameron Parish, Louisiana, which was made a year after Hurricane Clara, and Sauer (1972) suggests that the population was only ephemeral. This species occurs in pioneer beach vegetation from the Yucatan Peninsula northward along most of the Texas coastline.

In the genus there are two basic chromosome numbers, 16 and 17, evidently distributed without taxonomic significance. Nearly all species examined thus far are diploid with $2n = 32$ or 34 ; but *Amaranthus dubius* Mart. ex Thell., *A. giganteus* Koenig, and *A. caturtus* Heynh. are reported to be tetraploids with $2n = 64$.

Species of *Amaranthus* can be prolific seed producers. In a short note, G. N. Jones passed on the unpublished observations of C. F. Hottes that a single plant of *A. retroflexus* growing near Urbana, Illinois, in 1895 produced an estimated 2,359,000 seeds, and one of *A. albus* produced approximately 1,606,000.

Three (as delimited by Sauer) New World species of *Amaranthus* were domesticated as pseudo-grain crops before the Spanish Conquest: *A. hypochondriacus* in northwestern and central Mexico, *A. cruentus* in southern Mexico and Central America, and *A. caudatus* in the Andean highlands of South America. While the seeds of all wild and cultivated nongrain species of *Amaranthus* are blackish, those of species grown for their seeds are pale ivory; the oldest records for pale amaranth seeds are of *A. cruentus* from Coxcatlán Cave, near Tehuacán, Puebla, Mexico, at levels dated at about 4000 and 2500 B.C. At the time of the Conquest, *A. hypochondriacus* was a major grain crop in central Mexico. The plant also had considerable religious significance, since idols used in the most important ceremonies were made from the seeds. Because of this pagan usage, the cultivation of the "grain" amaranths was suppressed under Christianity, and today they are grown only vestigially in this hemisphere. The pseudo-grain amaranths, especially *A. hypochondriacus*, were carried very early to the Old World (early botanists considered them an Old World crop), and they are rather commonly cultivated there today, especially in the Himalayan region. The seeds of pseudo-grain amaranths are used in several ways: parched and milled into flour, cooked for gruel, popped and molded into cakes with syrup, or powdered and made into a drink. The nutritional value of the seeds is very high; of special importance is the high level of lysine, an essential amino acid in which most grains are deficient. Grain amaranths are considered a crop that could potentially be further developed through a breeding program to augment the few major grains suitable for developing countries.

Certain highly red-pigmented forms of *Amaranthus cruentus* were selected by Indians, and a dye used to color ceremonial wafers was extracted from the plants. Today, these red forms are cultivated in much of the world as potherbs and ornamentals. Red-pigmented forms of *A. caudatus* are also grown as ornamentals. *Amaranthus cruentus* is well known as a vegetable in Africa, as *A. tricolor* L. (*A. gangeticus* L.) is in Asia. *Amaranthus caudatus*, *A. inamoenus* Willd., *A. paniculatus* L., *A. tricolor*, and *A. viridis* are used as vegetables in China.

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3. *Achyranthes* Linnaeus, Sp. Pl. **1**: 204. 1753; Gen. Pl. ed. 5. 96. 1754, “*Achyranthes*.”

Annual or perennial herbs, sometimes suffrutescent at the base, with erect, ascending, or decumbent, simple to much-branched, glabrous to tomentose or sericeous, terete or quadrangular stems. Leaves opposite, petiolate [or sessile], the blades entire, elliptical to ovate, obovate, or orbicular. Inflorescences terminal and axillary, many flowered, mostly elongate, often interrupted spikes or panicles, only a few flowers open at the same time; bracts membranaceous, the bracteoles long-aristate and spinose. Flowers perfect, whitish, greenish, pinkish, or reddish, often becoming deflexed in age. Tepals 4 or 5, basally connate, coriaceous, becoming indurated in fruit, the segments narrow, nearly equal or not, acute, acuminate, or awned, pungent or not in fruit, glabrous or pubescent, with one or more prominent veins. Stamens 5, much shorter than tepals, the filaments alternating with pseudostaminodia, all connate below into a cup; filaments filiform; pseudostaminodia erose to lacinate, often with a prominent dorsal scale; anthers with 4 locules and 2 lines of dehiscence. Style 1, elongate, filiform; stigma 1, small, capitate; ovary obovoid, turbinate, or ovoid, slightly compressed, glabrous; ovule 1, pendulous from the tip of an elongate funiculus, the micropyle superior. Fruit an indehiscent, ovoid or obovoid, truncate or apically depressed, membranaceous utricle enclosed by the indurated tepals, falling off with the perianth and bracteoles; seeds obovoid or ovoid, smooth, inverted; embryo peripheral, surrounding the mealy perisperm, the cotyledons linear or lanceolate, flattened, the apices incurved from the erect radicle. (*Centrostachys* Wall. in Roxb.; not *Achyranthes* sensu Standley, Jour. Wash. Acad. Sci. **5**: 72. 1915, and N. Am. Fl.) LECTOTYPE SPECIES: *A. aspera* L.; see A. S. Hitchcock & M. L. Green, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 135. 1929, and A. A. Bullock, Kew Bull. **1957**: 73. 1957. (Name from Greek *achyron*, chaff, and *anthos*, flower.)

About 8–12 species mostly in the tropics, subtropics, and warm-temperate zones of the Old World (3 species occur in Japan), with *Achyranthes aspera* very widespread in both the Old and New Worlds. Townsend (1974b, family references) noted that *Achyranthes* is “a very difficult genus taxonomically, greatly in need of cytological and experimental investigation; there appear to have been a number of geographical races of, in particular, *A. aspera*; these, getting about as weeds, have probably interbred with local populations. The result has been a welter of forms virtually defying taxonomic treatment.”

There has been considerable nomenclatural confusion with regard to this genus, largely because Standley changed existing generic concepts by designating *Achyranthes repens* L. as the lectotype species of *Achyranthes* and

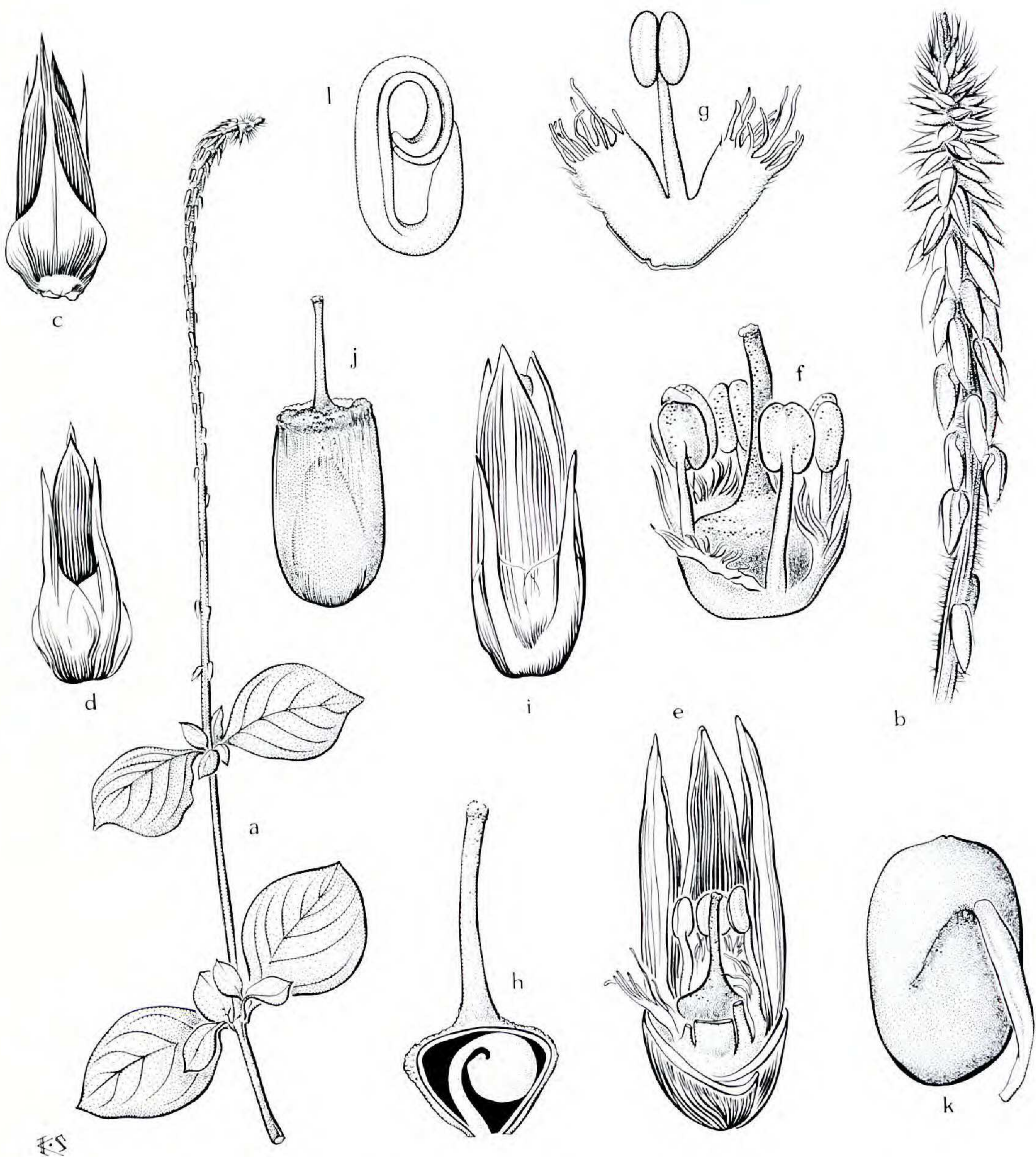


FIGURE 2. *Achyranthes*. a-l, *A. aspera*: a, upper part of flowering and fruiting stem, $\times \frac{1}{2}$; b, tip of same, $\times 2$; c, abaxial side of inflorescence bract and, in its axil, a flower, $\times 10$; d, adaxial side of same showing lateral, spinescent bracteoles, $\times 10$; e, flower with two tepals, two stamens, and pseudostaminode partly removed, $\times 12$; f, androecium and gynoecium removed from flower—note pseudostaminodia alternating with stamens, $\times 20$; g, adaxial side of part of androecial cup with one stamen and two pseudostaminodia, $\times 20$; h, gynoecium, part of ovary wall removed to show ovule suspended from tip of elongate funiculus, $\times 25$; i, mature fruit surrounded by accrescent, indurated tepals and spiny, lateral bracteoles, $\times 10$; j, mature utricle, $\times 12$; k, seed with persistent funiculus, tip of radicle visible through thin seed coat, $\times 15$; l, embryo removed from seed, $\times 12$.

transferring species previously referred to *Alternanthera* to *Achyranthes*; species that had been included in *Achyranthes* were placed by Standley in *Centrostachys* Wall. However, Bullock demonstrated that Standley's lectotypification of *Achyranthes* was incorrect and that the lectotype species should be *A. aspera* L. This essentially returned the concepts of these genera to those that had existed earlier. *Centrostachys* now includes only *C. aquatica* (R. Br.) Wall. ex Moq., which is frequently included within *Achyranthes*.

Achyranthes aspera L. (*Centrostachys aspera* (L.) Standley, *C. indica* (L.) Standley), $2n = 42$, occurs mostly in waste ground and old fields from southern Florida to southern Alabama and Texas; it is a pantropical weed, now being found in the West Indies and Central America, as well as in the Old World from the south coast of Europe to Africa and southern Asia. This is a very variable species in which numerous subspecific taxa have been proposed. Two leaf forms occur in our area: the one ovate to broadly ovate, acuminate, the other orbicular to obovate-orbicular, rounded and apiculate. The first has been called var. *aspera*, the second var. *indica* (L.) Miller. However, Cavaco (family references) concluded that the type material of *A. aspera* is from Ceylon and that the plants that have been called var. *indica* must now be referred to var. *aspera*. Townsend (1974a, family references) adopted the name *A. aspera* var. *pubescens* (Moq.) Townsend for the taxon previously known as var. *aspera*.

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Subfamily GOMPHRENOIDEAE Schinz

4. **Guilleminea** Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. **6**: ed. fol. 34, ed. quarto. 40. *pl.* 518. 1823; not *Guilleminea* Necker, 1790, *nomen illegit.*

Perennial herbs [rarely suffrutescent or caespitose] with numerous, much-branched, prostrate or ascending stems radiating from a stout taproot. Leaves opposite, entire, linear to lanceolate, spatulate, or ovate, of three types—large, elongate, persistent [or withering] basal leaves in a rosette, moderately large cauline leaves [members of each pair unequal], and small leaves subtending each inflorescence; blades long-tapering at base into a winged petiole. Inflorescences much-condensed spikes, rarely of solitary flowers, in axillary glomerules; each flower subtended by 2 bracts and 1 bractlet, all subequal, persistent, and membranaceous. Flowers perfect, minute, ± sessile. Tepals 5, ± equal, free [or the bases connate into a cup], abaxially lanate. Stamens 5; filaments connate below into a tube, the tube free from [or adnate to] the calyx; anthers with 2 locules and 1 line of dehiscence; staminodia and pseudostaminodia absent. Style 1, usually short; stigma capitate, inconspicuously bilobed; ovary compressed; ovule solitary, anatropous, pendulous from the tip of a long funiculus, the micropyle superior. Fruit a small, membranaceous, indehiscent utricle. Seed nearly filling the fruit, lenticular-orbicular, shiny reddish brown; embryo annular, surrounding the central, mealy perisperm, the radicle superior. (*Brayulinea* Small; including *Gossypianthus* Hooker, see Mears.) TYPE SPECIES: *G. illecebroides* HBK. =

G. densa (Willd. ex Roemer & Schultes) Moq.⁵ (Named for Antoine Guillemain, 1796–1842, French botanist, author, and explorer; in the dedication of the genus, particular mention was made of Guillemain's then unpublished observations on the Gentianaceae.) — COTTONFLOWER.

According to the latest revision (Mears), five species and ten varieties in two subgenera of the south-central and southwestern United States, Mexico, Hispaniola, Cuba, Colombia, Ecuador, Peru, Bolivia, Paraguay, Uruguay, and Argentina. The genus is represented in our area only by the occasional occurrence in Arkansas of *Guilleminea lanuginosa* var. *tenuiflora*.

Guilleminea lanuginosa (Poiret) Hooker f. is a variable species that ranges from western Arkansas and central Oklahoma through much of Texas to southwestern Chihuahua and central Tamaulipas; it also occurs in Hispaniola. Four varieties, distinguished mostly by the density of trichomes and the shape and size of the basal and cauline leaves, were recognized by Mears. Varietas *tenuiflora* (Hooker) Mears, a fairly large, often glabrous plant with ascending stems and linear radical leaves 40–90 mm. long, occurs in prairies and savannas from western Arkansas and central Oklahoma southward to southern Texas and Tamaulipas.

Guilleminea Brittonii (Standley) Mears, a Cuban endemic, is closely related to *G. lanuginosa*. Most authors have considered these two to comprise *Gossypianthus* Hooker, which was distinguished from *Guilleminea* by the persistent, rather than withering, basal leaves, and by the androecial tube being free from, instead of adnate to, the calyx. These characters are evidently subject to variation, however, and Mears considered *Gossypianthus* to be a subgenus of *Guilleminea*. The other species of *Guilleminea*, all belonging to subg. GUILLEMINEA, are *G. densa* (Willd.) Moq. (Oklahoma to Oaxaca, and disjunctly from southern Colombia to Argentina and Uruguay), *G. australis* (Griseb.) Hooker f. (Jujuy Prov., Argentina, and western Paraguay), and *G. elongata* Mears (Uruguay). In the checklist of Amaranthaceae in Kartez & Kartez (family references), of which the Gomphrenoideae were reviewed by Mears, *Gossypianthus* is again treated as distinct from *Guilleminea*.

Guilleminea has usually been referred to tribe Brayulineae Standley, along with *Tidestromia*. With the inclusion of *Gossypianthus*, Mears considered *Guilleminea* to be a member of tribe Gomphreneae Schinz.

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⁵Reed cites "*Paronychia lanuginosa* Poir." as the type of *Guilleminea*, but this is the basionym of the correct specific name for *Gossypianthus rigidiflorus* Hooker, which is the type species of the segregate genus *Gossypianthus* Hooker (= *G. lanuginosa* (Poiret) Hooker f. in Bentham & Hooker var. *rigidiflora* (Hooker) Mears).

5. *Tidestromia* Standley, Jour. Wash. Acad. Sci. 6: 70. 1916.

Annual [or perennial] herbs, sometimes suffruticose at base; stems much branched, prostrate or ascending, radiating from a slender to thick caudex and taproot [or from horizontal rhizomes]; indumentum of stellate or branched trichomes. Leaves opposite, entire, petiolate, decreasing in size toward tips of branches, the blades broadly ovate, orbicular, or spatulate with truncate to tapering bases and rounded to slightly acute apices; bases of the uppermost leaves \pm connate and indurated, forming an involucre. Inflorescences axillary glomerules, bracteate and bibracteolate, the bracts and bracteoles hyaline and pubescent. Flowers perfect, minute. Perianth segments 5, distinct, the outer 3 wider than the inner 2, membranaceous, glabrescent or villous. Androecium of 5 hypogynous stamens; filaments connate below into a cup with or without intervening lobes or pseudostaminodia; anthers with 2 locules and 1 line of dehiscence. Ovary globose; styles short; stigmas capitate or 2-lobed; ovule 1, suspended from the apex of a slender, elongate funiculus. Utricle slightly compressed, glabrous, indehiscent; seeds globose, brown. (*Cladothrix* (Nutt. ex Moq.) S. Watson, 1880, not Cohn, 1875, Schizomycetes; *Alternanthera* sect. *Cladothrix* Nutt. ex Moq.) TYPE SPECIES: *Alternanthera lanuginosa* (Nutt.) Moq. in DC. = *Tidestromia lanuginosa* (Nutt.) Standley.⁶ (Name commemorating Ivar Tidestrom, 1864–1956, Swedish-born American botanist noted for floras of the southwestern United States.)

About six species of southwestern North America, with *Tidestromia lanuginosa* occurring eastward to Cameron and Sabine parishes, Louisiana. The species is evidently native to these localities since it occurs in nearby coastal Texas. It ranges from South Dakota and Kansas to Utah and Nevada, south to Texas, Arizona, northern Mexico and Hispaniola; it is adventive in Missouri and Illinois. The plant occurs in disturbed or severe habitats, such as roadsides, clay banks, limestone-sandy soil, gypsum and gravel washes, and valley silts. Kearney & Peebles noted that it forms conspicuous white mats soon after summer rains on deserts in southern Arizona and that it is adapted for checking the blowing of sandy soils. This species is distinguished from others of the genus by its annual habit and by the absence of pseudostaminodia or the presence of only very short ones. The plants of our area correspond to var. *lanuginosa*, which is characterized by gray-green foliage with stellate trichomes. This variety is distributed throughout the range of the species. Varietas *carnosa* (Steyermark) Cory, with yellowish green, nearly glabrous foliage and very brittle stems, occurs in gypseous saline soils from southern and western Texas southward to Chihuahua, Mexico; it is sometimes recognized as a distinct species, *T. carnosa* (Steyermark) I. M. Johnston.

The genus has not been reviewed throughout its entire range. The other species usually recognized are *Tidestromia gemmata* I. M. Johnston (gypsiferous shales, southwestern Texas and northern Mexico); *T. oblongifolia* (S. Watson) Standley, with subsp. *oblongifolia* (eastern Mojave and Colorado

⁶Only *Alternanthera lanuginosa* was included in sect. *Cladothrix* by Moquin; thus, it is the type of subsequent names based on this section.

deserts eastward into Nevada and Arizona) and subsp. *cryptantha* (S. Watson) Wiggins (western Colorado Desert near the Salton Sea and adjacent slopes); *T. suffruticosa* (Torrey) Standley, with var. *suffruticosa* (rocky soils containing some gypsum, western Texas and southern New Mexico to Coahuila) and var. *coahuilana* I. M. Johnston (somewhat gypseous soil, Coahuila); *T. rhizomatosa* I. M. Johnston (probably a halophytic gypsophile, Coahuila); and *T. tenella* I. M. Johnston (probably gypsophilous, Coahuila).

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6. *Froelichia* Moench, Method. 50. 1794.

Annual [or perennial] herbs [or shrubs] with semi-woody taproots; stems simple to much branched, erect or procumbent, usually densely pubescent. Leaves opposite, short-petiolate [or sessile], most abundant on the lower half of plant, the blades entire, woolly, densely pubescent. Inflorescences interrupted simple or compound spikes mostly on long, erect peduncles; each flower subtended by an adaxial bract persistent on the peduncle and by 2 lateral bracteoles that detach with the fruit. Flowers perfect, sessile. Tepals 5, connate into a 5-lobed perianth tube, the lobes lanceolate, acute, glabrous, and greenish white or pinkish and the tube lanate, becoming indurated in fruit and bearing crests or tubercles. Stamens 5; filaments connate into a tube with the 5 anthers sessile between the 5 lobes of the staminal tube; anthers with 2 locules and 1 line of dehiscence. Style 1, somewhat elongate [or nearly absent], shorter than the staminal tube; stigma sessile, capitate, irregularly lobed [or penicillate]; ovary ovoid; ovule solitary, pendulous from the tip of a long funiculus, the micropyle superior. Fruit a small, ovoid, membranaceous, indehiscent utricle enclosed by the indurated perianth tube; mature perianth tube with 2 longitudinal rows of spines or irregularly toothed wings and 3 basal tubercles; seed obovoid or lenticular, smooth, inverted;

embryo annular, surrounding the central, mealy perisperm, the radicle superior; usually germinating while enclosed by the perianth tube. (*Oplotheca* Nutt., *Hoplotheca* Sprengel, *Ninanga* Raf., and *Everior* Raf.) TYPE SPECIES: *F. lanata* Moench = *F. interrupta* (L.) Moq. in DC. (Name honoring Joseph Aloys Froelich, 1766–1841, German physician and botanist who published on *Sonchus*, *Hieracium*, and *Gentiana*.) — COTTONWEED, SNAKEWEED.

Perhaps 12 species of the eastern, central, and southwestern United States; Mexico; most of the Greater Antilles; the Galapagos Islands; and South America from Colombia to Paraguay, Chile, Brazil, and Argentina. Six species occur in North America, two in our area. The greatest diversity appears to be in southwestern North America and in Brazil. A modern review of the genus is needed (the last was by Schinz, 1933), particularly in terms of the relationships of the species of South America and those of southwestern North America.

Froelichia gracilis (Hooker) Moq. is distinguished from other species of the genus by its asymmetrically conical fruiting perianths less than 4 mm. long with crests of lateral rows of distinct spines, tannish seeds, leaves mostly 5–10 mm. wide, and stems much branched from the base. This species occurs mostly in sandy soil from Iowa to Colorado, southward to Arkansas, Texas, New Mexico, and Mexico; it is widely adventive eastward to Wisconsin, Illinois, Indiana, New York, New Jersey, Maryland, Virginia, North Carolina, South Carolina, Georgia, Alabama, and Mississippi. In areas where it is introduced, it is usually found along railroad tracks in cindery soil.

Froelichia floridana (Nutt.) Moq. (leaves mostly 10–30 mm. wide; mature fruiting perianths over 5 mm. long, flask shaped, the crests deeply dentate with irregular margins; seeds dark red-brown; stems branching profusely only in the upper nodes) occurs from Delaware, New Jersey, Indiana, Minnesota, South Dakota, and Colorado to Florida, Mississippi, and Texas. Two distinct varieties are recognized. *Varietas floridana* has taper-tipped elliptic-lanceolate leaves that are canescent to subscabrous above, puberulent or tomentulose branches with short trichomes, and peduncles with trichomes less than 0.5 mm. long. This variety occurs on the Coastal Plain from Florida north to Delaware and New Jersey, and west to Mississippi and Texas. *Varietas campestris* (Small) Fernald (*F. campestris* Small) has oblanceolate or subspathulate, obtuse-tipped leaves that are canescent or silky on the upper surface, sericeous-tomentose branches, and lanate peduncles with the trichomes commonly 2 mm. long; it ranges from Indiana, Wisconsin, Minnesota, and South Dakota, southward to Illinois, Missouri, Kansas, Arkansas, Oklahoma, Texas, and Colorado. Both varieties are usually found in sandy soil.

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7. **Alternanthera** Forsskål, *Fl. Aegypt. Arab.* 28. 1775.

Annual or perennial herbs [shrubs or rarely small trees]; stems prostrate, decumbent, ascending, erect, or floating, often pubescent with simple, dentate, or barbed trichomes; taproot often present and robust. Leaves opposite, entire, sessile or petiolate, the blades narrow to broad. Inflorescences axillary or terminal, sessile or pedunculate, globose or cylindrical, usually whitish or silvery headlike spikes; bract and bracteoles scarious, the latter keeled. Flowers perfect, or imperfect by malformation. Perianth often dorsally compressed, of 5 free, equal or unequal, glabrous or variously pubescent tepals, 2 more concave than the rest. Stamens usually 5, sometimes anthers missing from some filaments; filaments connate basally into a tube or short cup; pseudostaminodia 5, ligulate, subulate, or reduced to small teeth, or rarely absent, entire to lacinate, alternating with antheriferous filaments on the androecial tube; anthers with 2 locules and 1 line of dehiscence. Ovary globose or ovoid, compressed or not; style usually short; stigma capitate, seldom bilobed, the papillae often elongate; ovule 1, suspended from the tip of an elongate, basal funiculus, the micropyle superior; spurious carpels sometimes produced on androecial tube. Utricle compressed, ovoid or obovoid, sometimes corky, falling off with the perianth and with or without the bracteoles, the margin often narrowly winged, seed lenticular, and seed coat semipellucid or coriaceous, smooth; embryo annular, surrounding the mealy perisperm, the cotyledons narrow, the radicle superior. (*Achyranthes* sensu Standley, *Jour. Wash. Acad. Sci.* **5**: 72. 1915, not L., 1753; *Telanthera* R. Br.) TYPE SPECIES: *Gomphrena sessilis* L. = *A. sessilis* (L.) DC.; see R. Melville, *Kew Bull.* **13**: 171. 1958. (Name from Latin *alternans*, alternating, and *anthera*, anther, referring to the alternation of pseudostaminodia with antheriferous filaments). — CHAFF FLOWER.

Approximately 80 species according to Mears, but some estimates as high as 200. The vast majority of species occur in the American tropics and subtropics, with a few in Africa, Asia, and Australia; 16 species or subspecies, 11 of them endemic, occur in the Galapagos Islands. Several species are

aggressive weeds that have become naturalized in many parts of the world. Since Moquin-Tandon's treatment of the family for De Candolle's *Prodromus* (1849), the genus has been revised only regionally. As recent investigators have examined species over broader geographic areas, there have been numerous name changes; there will doubtless be more as revisionary work continues. The genus has been divided into several sections, but because of the present lack of knowledge of many species, subdivisions are not recognized in most floristic works. Seven species (three of them introduced) occur in the southeastern United States. See the discussion under *Achyranthes* concerning Standley's unfortunate application of that name to this genus.

Two species in our area have long-pedunculate axillary and terminal inflorescences. *Alternanthera philoxeroides* (Mart.) Griseb. (*Achyranthes philoxeroides* (Mart.) Standley), alligator weed, $2n = 28, 100$, a native of South America, has become naturalized in ponds, ditches, streams, and bayous on the Coastal Plain from North Carolina to Florida, west to Louisiana and southeastern Texas; it occurs also in much of South America and is widely scattered, but infrequent, in Central America and the West Indies, and in parts of the Old World. This vigorously growing plant, along with water hyacinth (*Eichhornia crassipes*, Pontederiaceae), clogs waterways in the southeastern United States. It is an aquatic to semiterrestrial perennial herb, often forming mats, with sessile flowers and linear to lanceolate-ovate leaf blades; the stems (except for the upper internodes), tepals, and leaves are nearly glabrous. *Alternanthera flavescens* HBK. (*A. ramosissima* sensu auct.), with shortly pedicellate flowers, ovate or elliptic leaves, and pubescent stems and tepals, occurs in coastal hammocks and thickets and on sand bars in southern Florida; it also occurs in Mexico, the West Indies, and South America.

The other species of *Alternanthera* in our area have inflorescences that are essentially sessile (the peduncles less than 1 cm. long) in the axils of leaves. Three have elongate androecial tubes with the pseudostaminodia lacinate and equaling or exceeding the filaments. *Alternanthera maritima* (Mart.) St. Hil. (*Achyranthes maritima* (Mart.) Standley, *Telanthera maritima* (Mart.) Moq.), with procumbent or prostrate stems, fleshy ovoid leaves, and glabrous, rigid, striate tepals, occurs along sandy beaches and in hammocks in southern peninsular Florida; it also is found in Bermuda, the West Indies, Brazil, and West Africa. *Alternanthera tenella* Colla (*A. ficoidea* sensu many authors, not (L.) Beauv.; see Veldkamp, Mears), with erect stems, nonfleshy, green leaves, and sparsely pilose, marginally chartaceous tepals, may be locally naturalized in our area, but I have seen no documenting specimens. This variable species of Mexico, Central America, South America, and the West Indies is often divided into several varieties or segregate species. A related species, *A. Bettzichiana* (Regel) Voss (*Achyranthes Bettzichiana* (Regel) Standley; including *Al. amoena* (Lem.) Voss), parrotleaf, calico plant, a widely cultivated, variable plant, often with brightly colored foliage, is native to Brazil but has escaped in many parts of the world, including southern Florida. (See Mears regarding the spelling *Betzichiana* vs. *Betzickiana*.)

The three other species of *Alternanthera* in our area have short androecial tubes and pseudostaminodia that are entire or dentate and shorter than the

staminal filaments. *Alternanthera paronychioides* St. Hil. (*A. polygonoides* (L.) R. Br.; *Achyranthes polygonoides* (L.) Lam., *Gomphrena polygonoides* L., *pro parte*, see Pedersen, 1967), $2n = 34, 96$, distinguished by its \pm equal tepals 3–5 mm. long that lack rigid, spinose tips and by leaves that are

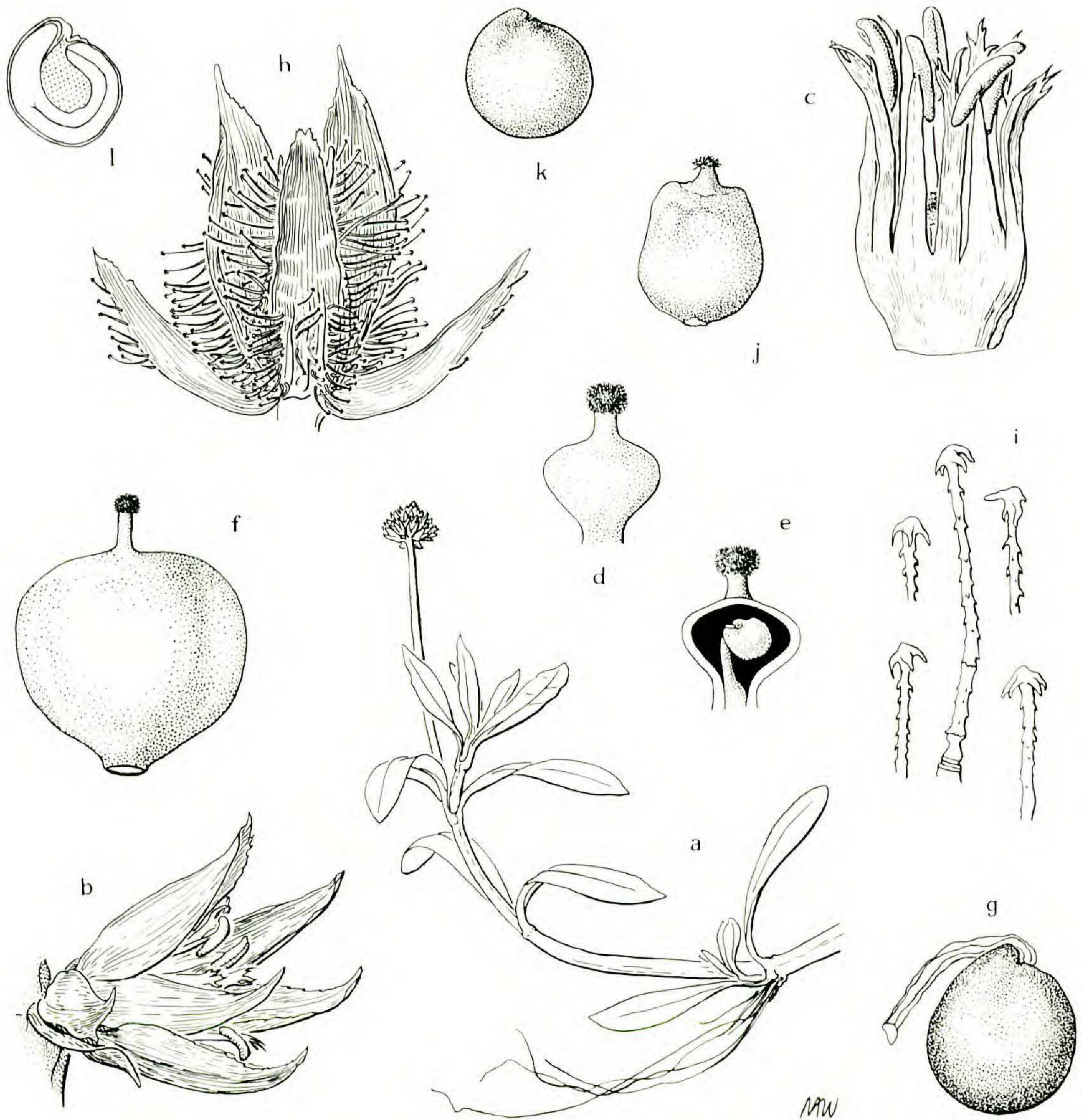


FIGURE 3. *Alternanthera*. a–g, *A. philoxeroides*: a, tip of stem with inflorescence, $\times \frac{1}{2}$; b, lateral view of flower showing subtending bract and one of two lateral bracteoles, $\times 5$; c, androecium with five fertile stamens alternating with five pseudostaminodia (stigma barely visible within), $\times 10$; d, gynoecium, $\times 10$; e, same, with part of ovary wall removed to show ovule on elongate funiculus, $\times 10$; f, fruit (from an Uruguayan specimen), $\times 8$; g, seed with persistent funiculus (also from Uruguay), $\times 8$. h–l, *A. caracasana*: h, flower from above to show two lateral bracteoles and heteromorphic tepals, $\times 10$; i, glochidiate trichomes from tepals, $\times 48$; j, fruit, $\times 10$; k, seed, funiculus removed, $\times 10$; l, diagrammatic vertical section of seed, perisperm stippled, $\times 10$.

about twice as long as broad, occurs near salt water from North Carolina to southernmost Florida, west to Alabama, Louisiana, and Texas; it is also found in Mexico, Central America, South America, the West Indies, Africa, and India, and on some Pacific islands. *Alternanthera pungens* HBK. (*A. repens* (L.) Link, not Gmelin nor American authors, see Melville; *Achyranthes leiantha* (Seub.) Standley), $2n = 64$, with spinose-tipped, sparsely villous tepals 4–7 mm. long, leaf blades as long as broad (up to 2×2 cm.), and dentate pseudostaminodia, is a variable South American species that is adventive in Florida, Alabama, and Texas; it is also found in Cuba, Jamaica, Africa, India, Thailand, Australia, and Hawaii. *Alternanthera caracasana* HBK. (*Achyranthes repens* sensu American authors, not L.; *Al. peploides* (Willd. ex R. & S.) Urban), with spinose-tipped, densely villous tepals 3–5 mm. long, leaf blades longer than broad (up to 1.5×1 cm.), and entire pseudostaminodia, ranges from South Carolina to Florida, west to Texas and California; it also occurs in South America, Africa, and the Canary Islands.

Alternanthera philoxeroides was first reported in the southeastern United States in Florida in 1894. Since then it has spread northward along the Coastal Plain to North Carolina and Virginia and westward to Tennessee, Arkansas, and Texas; it has also become established locally in southern California. It has been estimated that by 1970 the plant had infested between 27,000 and 65,700 hectares (66,770 to 162,000 acres) of water in North and South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, and Texas. Reproduction is by fragments of plants (viable seeds are evidently not produced in the United States). The species occurs in moist soil along bodies of water, rooted in shallow water, or in floating mats in deeper water, in which the interwoven stems may extend 1 m. or more down into the water and up to 100 m. over the surface. Native vegetation cannot compete with the weed, so nearly pure stands are formed, unlike the almost inconspicuous occurrence of the plant in undisturbed habitats in southern South America. Chemical herbicides are not consistently effective in controlling it, and there are no serious natural insect pests in the United States. Since 1964, three South American insects have been released as biological control organisms in the United States: *Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae), alligatorweed flea beetle; *Amynothrips andersoni* O'Neill (Thysanoptera: Phlaeothripidae), alligatorweed thrips; and *Vogtia malloi* Pastrana (Lepidoptera: Pyralidae: Phycitinae), alligatorweed stem borer. "These insects are now providing substantial control of alligatorweed over the entire range where the weed occurred as an aquatic plant problem. It is our contention that alligatorweed will cease to be an important aquatic weed and only rarely will be found in pure stands in any significant proportions in the United States of America" (Spencer & Coulson).

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8. **Gomphrena** Linnaeus, Sp. Pl. **1**: 224. 1753; Gen. Pl. ed. 5. 105. 1754.

Annual or perennial herbs [caespitose subshrubs, or lianas], the stems usually pubescent and much branched from near base and wide spreading, ascending, decumbent, prostrate, or erect, sometimes rooting at the nodes; nodes often swollen; [roots often tuberous or a deep taprootlike caudex]. Leaves opposite [alternate, fascicled, or mostly basal], shortly petiolate or sessile [often partly clasping at base], the blades entire, ovoid to obovate [linear, lanceolate, or circular], usually pubescent at least below. Inflorescences of terminal and/or axillary, many-flowered, sessile [to long pedunculate], subglobose [discoid or cylindrical] heads [or short to elongated spikes], often subtended by an involucre of sessile leaves, the heads solitary [or forming an interrupted spike or arranged in open panicles]; bracts and bracteoles thin [to scarious or subcoriaceous], white or colored [often brilliantly], the bracts persistent, glabrous [or sparsely pubescent], strongly concave or folded, the bracteoles glabrous, \pm deciduous, usually longer than the bracts and equaling [or exceeding] the tepals, the abaxial surface often with a denticulate, laciniate [serrate, or entire] crest. Flowers perfect. Tepals

white [or colored], connate below [or free], strongly concave, scarious, abaxially densely long-pubescent [rarely glabrous], entire [or serrate]. Androecium of 5 monadelphous stamens, the tube included [or exerted], sometimes slightly adaxially curved, white to \pm colored, containing nectar; each free filament segment mostly 3-parted at the apex with 2 variously shaped lateral lobes and a central, slender, often very short antheriferous lobe; anthers introrse, dorsifixed, oval to linear, with 2 locules and 1 line of dehiscence; pseudostaminodia absent. Style 1, \pm elongate [to very short or absent], usually included within staminal tube; stigmas 2 or rarely 3 [or 1 and then bilobed], the branches mostly erect, slender and subulate or filiform; ovary subglobose [ovoid, turbinate, or cylindrical], slightly compressed; ovule 1, suspended from the apex of an elongated, basally attached funiculus, the micropyle superior; base of ovary surrounded by a prominent disc. Fruit an ovoid or oblong, somewhat compressed, indehiscent utricle usually included within the persistent tepals and staminal tube, the fruit wall very thin, membranaceous; seed lenticular, smooth, lustrous, reddish brown [brown, or yellowish], the seed coat coriaceous; embryo annular around the mealy perisperm, the cotyledons obovate or narrow, the radicle slender, superior. LECTOTYPE SPECIES: *G. globosa* L.; see P. C. Standley, N. Am. Fl. **21**: 147. 1917, and A. S. Hitchcock & M. L. Green, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 137. 1929. (Name perhaps a modification of the Latin name, *gromphaena*, used by Plinius for a kind of amaranth; from Greek *gomphros*, "clavis ligni," according to Linnaeus.) — GLOBE-AMARANTH.

An estimated 100 species, originally restricted to the tropics, subtropics, and warm-temperate regions of the New World, except for approximately 18 species essentially of Australia. The last complete taxonomic treatment of the American taxa (Holzhammer, 1955) recognized 95 species in five sections; Mears (1980) has reviewed those originally described by Linnaeus as species of *Gomphrena*.

In our area, apparently indigenous plants of *Gomphrena* occur along roadsides, ditches, beaches, and in waste areas in peninsular Florida. These have been recognized as two species, *G. decumbens* Jacq., $2n = 18, 26$, and *G. dispersa* Standley, considered by Holzhammer to be closely related species of sect. GOMPHRENA. Mears, however, includes both of these within *G. serrata* L., "the most common and most widely distributed noncultivated species of *Gomphrena*." The general distribution of *G. serrata* is in Florida, southern Texas, the Greater Antilles, Mexico, Central America, and (apparently disjunctly) in Bolivia and Paraguay. *Gomphrena globosa* L., globe-amaranth, $2n = 44$, is very commonly cultivated in our area and may persist after or escape from cultivation; it was collected in St. Landry Parish, Louisiana, by Correll and Correll (9468, GH).

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9. **Iresine** P. Browne, *Civil Nat. Hist. Jamaica*, 385. 1756, nomen conserv.

Annual or perennial herbs [subshrubs, shrubs, or small trees] from taproots, horizontal rhizomes [or branching rootstocks], the stems ± pubescent or glabrous, unbranched to much branched, erect to prostrate, often trailing, the nodes somewhat swollen. Leaves opposite, petiolate, the blades thin [to somewhat fleshy], entire or serrulate. Inflorescences of small, crowded spikes [or heads] arranged in many-flowered, mostly open panicles terminating stems and in axils of upper leaves; each flower subtended by a bract and 2 bracteoles, all membranaceous, shining, silvery white [stramineous or fuscous], glabrous to slightly [or densely] pubescent. Flowers small or minute,

usually imperfect and the plants monoecious, dioecious, or polygamous. Perianth of 5 basally connate or free, subequal, membranaceous, silvery white to stramineous, 1- to 3-nerved, abaxially glabrous or pubescent tepals, those of the carpellate flowers subtended by a ring of trichomes that elongate greatly in fruit. Androecium mostly of 5 stamens (these greatly reduced or lacking in carpellate flowers), the filaments basally connate, the anthers introrse, dorsifixed, with 2 locules and 1 line of dehiscence; pseudostaminodia absent or short. Style 1, very short or absent; stigmas 2 or 3, usually elongate, stout to filiform; ovary compressed in carpellate flowers, absent or rudimentary in staminate flowers; ovule 1, suspended from the top of the ovary by an elongate funiculus, the micropyle superior; all flowers with a prominent, 5-lobed disc. Fruit a very small, indehiscent, membranaceous, silvery white, \pm globose utricle subtended by copious very long trichomes and at maturity falling away from the bracts; seed smooth, lenticular, inverted, reddish to red-brown; embryo annular around the mealy perisperm; cotyledons narrow, the radicle superior. TYPE SPECIES: *Celosia paniculata* L. = *I. diffusa* Humb. & Bonpl. ex Willd. (Name evidently derived from Greek *eiresione*, a wreath or staff wrapped with fillets of wool, perhaps for the ring of long trichomes that subtend the tepals of many species.) — BLOODLEAF.

Perhaps 70 species mostly of the tropics and subtropics of the New World; also in Australia and the Galapagos Islands. Two species are indigenous to the southeastern United States.

Iresine diffusa Humb. & Bonpl. ex Willd.⁷ (*I. paniculata* (L.) Kuntze not Poiret, *I. Celosia* L., *I. celosioides* L., *I. canescens* Humb. & Bonpl. ex Willd.), commonly called "Juba's bush," a dioecious, annual herb (sometimes persisting for several years from a vertical rootstock) with erect, spreading, or clambering, much-branched stems and 3-nerved tepals that exceed the utricle, occurs in hammocks, marshes, and other habitats, mostly along the coast, supposedly from North Carolina southward to Florida and west to Texas; it also occurs in the West Indies, Mexico, Central America, and much of South America. Although reported from North Carolina by Reed (1969), Standley (1917), and Small (Man. S. E. Fl.), it was not included by Radford, Ahles, & Bell in their *Manual of the Vascular Flora of the Carolinas*.

Iresine rhizomatosa Standley (*I. paniculata* sensu Uline & Bray, not L.; *I. Celosia*, in part, of American authors, not L.; *I. celosioides* Michaux, not L.), a perennial, dioecious, stoloniferous herb with the erect stems largely unbranched below the inflorescence and with 1-nerved tepals that are shorter than the utricles, is mostly found in sandy alluvial soils of low woods and in depressions and sand dunes and along rivers from Maryland, southeastern Virginia, coastal North and South Carolina, Georgia, Florida, and Alabama, westward to Tennessee, southern Illinois, Missouri, Arkansas, southern

⁷Mears and Gillis adopt the name *I. canescens* Humb. & Bonpl. ex Willd. for this species; however, Shinner's usage of *I. diffusa*, which dates from the same time as *I. canescens*, must be followed in accordance with Article 57 of the International Code of Botanical Nomenclature.

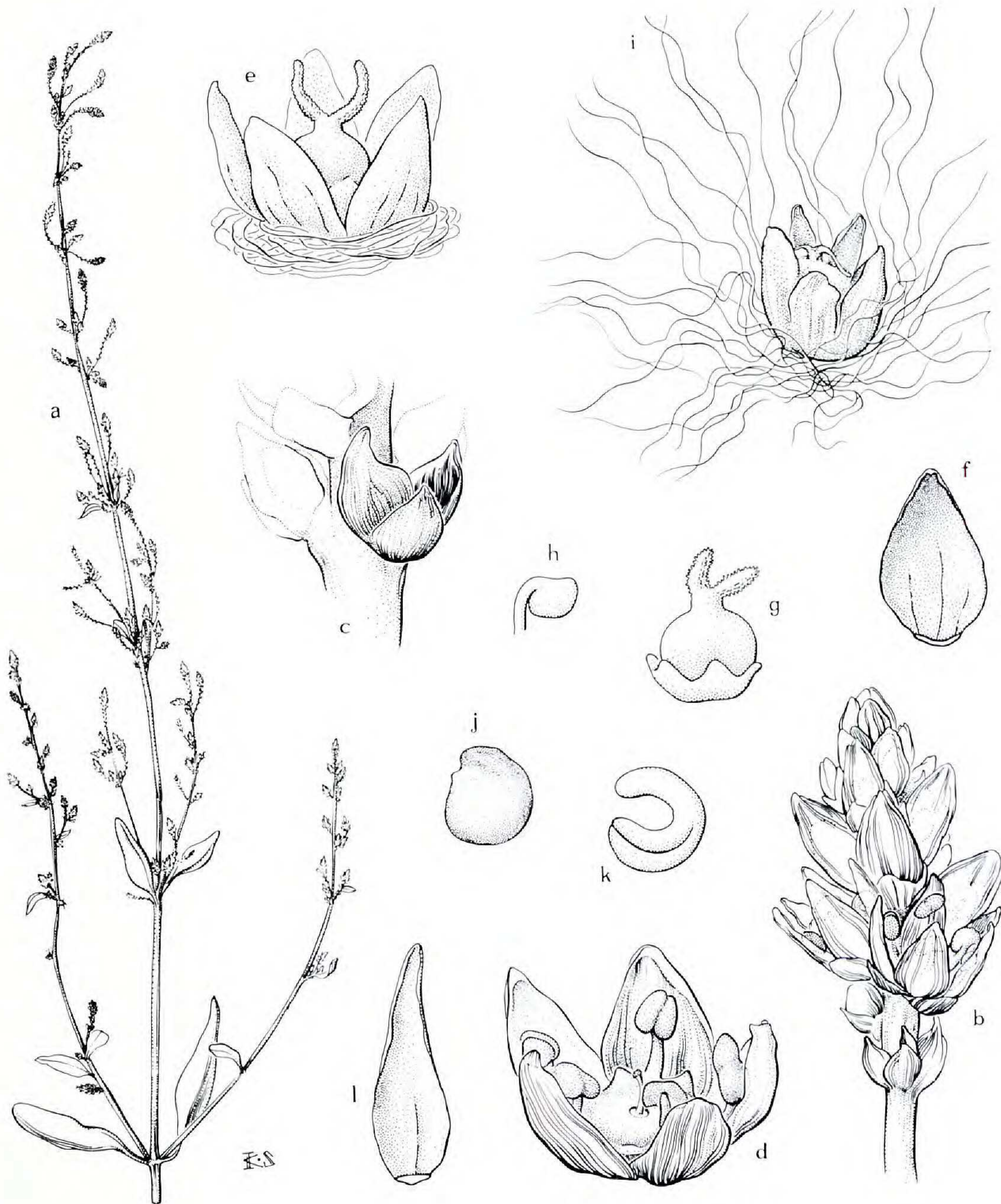


FIGURE 4. **Iresine.** a-k, *I. diffusa*: a, top of staminate plant, $\times 1/2$; b, tip of shoot with staminate flowers, $\times 12$; c, bracts subtending staminate flowers, flowers removed, $\times 25$; d, staminate flower, stamens opposite tepals—note rudimentary gynoecium in center of flower, $\times 25$; e, carpellate flower, surrounded at base by swirl of subtending trichomes, $\times 25$; f, tepal of carpellate flower—note three veins, $\times 25$; g, gynoecium with disc at base, $\times 25$; h, ovule and funiculus, $\times 25$; i, mature fruit with persistent tepals and unfurled subtending trichomes, $\times 12$; j, seed, $\times 25$; k, embryo, oriented as in "j," $\times 25$. l, *I. rhizomatosa*: tepal of carpellate flower showing single vein, $\times 25$.

Louisiana, Oklahoma, and southeastern Texas.

Standley (1917, family references) attributed *Iresine flavescens* Humb. & Bonpl. ex Willd. to southern Florida, but I have seen no specimens to document this; Mears & Gillis consider the species to be endemic to the West Indies.

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10. *Philoxerus* R. Brown, Prodr. Fl. Novae Holland. 416. 1810.

Procumbent or creeping, much-branched, somewhat succulent or fleshy, perennial or annual herbs [or low shrubs], the branches often ascending. Leaves opposite, sessile, thick and fleshy [or not], linear to narrowly obovate [or subulate], amplexicaulous, entire, glabrous except for tufts of trichomes in the axils. Inflorescences headlike or cylindrical [to elongate], many-flowered, pedunculate spikes solitary and terminal on branches; bracts and bracteoles chartaceous, 1-nerved, the bract expanded, the 2 bracteoles keeled. Flowers perfect, silvery white or pink, the pedicels very short, thick, white-lanate. Perianth of 5 unequal, dorsiventrally compressed, chartaceous, basally thickened and connate tepals, the outer 3 glabrous, the inner 2 abaxially lanate at the base. Stamens 5, filaments included, connate below into a short cup; anthers much shorter than the filaments, with 2 locules and 1 line of dehiscence; pseudostaminodia absent. Ovary dorsiventrally compressed, broadly ovoid; style very short; stigmatic branches 2 or 3, subulate; ovule solitary, pendulous from the tip of an elongate funiculus. Utricle somewhat compressed, broadly ovoid, coriaceous, thin, indehiscent or tearing irregularly; seed orbicular or lenticular, smooth, the seed coat coriaceous, lustrous brown, inverted; embryo annular around the mealy perisperm, the cotyledons narrow, the radicle superior. LECTOTYPE SPECIES: *P. conicus* R. Br.; see P. C. Standley, *N. Am. Fl.* **21**: 168. 1917. (Name evidently derived from Greek *philos*, loving, and *xeros*, dry, in reference to the habitat of species of the genus.)

As presently recognized, approximately 10 species, mostly littoral, in the tropics and subtropics of the Atlantic and Caribbean regions of the Americas, and western Africa, northern Australia, the Ryukyu Islands, and the Galapagos Islands. However, Mears (1980) says that the three Australian species originally placed in *Philoxerus* by Brown are now generally placed in *Gomphrena*, and

that it is necessary to revive the name *Caraxeron* Vaill. ex Raf. for the species now known as *Philoxerus vermicularis* (L.) J. E. Sm. and its relatives. Mears⁸ is preparing a paper about this change, and the name *Caraxeron vermicularis* (L.) Raf. was used for this taxon in Kartez & Kartez (family references).

Philoxerus vermicularis (L.) J. E. Sm.,⁹ silverhead, saltweed, samphire, a much-branched, perennial or sometimes annual herb with mostly prostrate stems, ascending branches, and globose to cylindrical, compact inflorescences that are white or pinkish when alive, drying silvery white, occurs in saline soils and sand of beaches, dunes, and sand bars along both eastern and western coasts of Florida, to Louisiana and Texas; it also ranges southward through Mexico to Panama, Colombia, and Brazil, in the West Indies, and on the western coast of tropical Africa.

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⁸Note added in proof: Mears (pers. comm.) has had two papers accepted for publication in *Taxon*, one treating the Australian species as *Philoxerus*, and the other placing the American species in *Blutaparon* Raf. instead of *Caraxeron* since Rafinesque included both the Australian and the American species in *Caraxeron*.

⁹The transfer of *Gomphrena vermicularis* L. to *Philoxerus* is usually attributed to R. Brown, Prodr. 416. 1810, but Brown merely indicated that *G. vermicularis* seemed to belong to *Philoxerus* and did not make the formal transfer. The first transfer appears to be by J. E. Smith in Rees, Cyclop. 27 [alph. ord.]. 1814, as *P. vermiculatus*, sphalm.